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First report on Rhabdocoela (Rhabditophora) from deep parts of Skagerrak, with the description of four new species

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Abstract

In this contribution we report on 13 species of Rhabdocoela, found during a marine inventory of Skagerrak by the Swedish Taxonomy Initiative. Four new species are described, two of which are Kalyptorhynchia (Gnathorhychidae and Polycystididae) and two belong to Dalytyphloplanoida (Solenopharyngidae). *Uncinorhynchus vorago* **sp. nov.**, (Gnathorhynchidae) has a triangular stylet consisting of a double-folded plate, which proximally forms a tube, but without a distal, needle-shaped tip. *Austrorhynchus artoisi* **sp. nov.** (Polycystididae), has two prostate stylets. Prostate stylet type II consists of a distal tube and a short proximal funnel, which has a stirrup-shaped ornament, whereas the stylet type III shows an unpronounced foot and style connected to each other by a narrow clasp and a comb-bearing plate. The foot and plate are connected to a thread-like flagellum. *Lenopharynx bathos* **sp. nov.** (Solenopharyngidae) resembles *Lenopharynx tubatus* Schockaert & Martens, 1985, but differs in the detailed structure of the stylet and by the lack of colouration and eyes. *Proceropharynx profundum* **sp. nov.** has a unique combination of small spines and hard ridges on the cirrus. Additional data are given for the remaining nine species, three of which are new for the Swedish fauna. *Espegrendia norvegica* Westblad, 1954 (Solenopharyngidae) is redescribed. For the sake of completeness, two more species are mentioned. One is identified as a new species of *Acrumena* Brunet, but lack of material prevents its formal description. The second one is probably a representative of the taxon *Ceratopera* Den Hartog, but cannot be identified with certainty because of the poor quality of the preserved material. This contribution is one of very few reports on Rhabdocoela collected from a depth exceeding 100 m and some preliminary biogeographical remarks are therefore given.

Key words: Platyhelminthes, turbellaria, Kalyptorhynchia, Dalytyphloplanida, taxonomy, biodiversity, deep-water

Introduction

Most studies dealing with marine rhabdocoels concern littoral and sublittoral localities down to 20 m depth. Records of rhabdocoels from locations with a depth range between 20 and 100 m are scarce (e.g. Karling 1952a, 1953, 1967, 1974; Noldt 1989 a-b, Willems *et al.* 2004a). There are very few reports of rhabdocoel species from depths exceeding 100 m, the only ones coming from some subantarctic islands (125-350 m; Reisinger 1926; Karling 1952a; Westblad 1952), the Weddell Sea (265-600 m; Artois *et al*. 2000), the Arctic (110-300 m; Steinböck 1932) and the Norwegian coast (Westblad 1954; Rieger & Sterrer 1975). These few deepwater surveys have revealed a total of 21 species of Rhabdocoela, of which 12 were newly described in the above mentioned reports. Furthermore, some yet undescribed species were collected at a depth of 2000 m (Artois *et al*. 2000), which indicates that there is a large potential of finding new rhabdocoel species in deeper waters.

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Sampling of littoral and shallow water rhabdocoels in the Skagerrak area has been done on several occasions (see Karling 1974 and references therein). However, nothing is known about the rhabdocoels of the deeper parts of Skagerrak.

The Swedish Taxonomy Initiative (ArtDatabanken) recently started a series of marine inventories along the Swedish west coast in Skagerrak and Kattegat. The present contribution reports on 13 species of rhabdocoels collected in the deep waters of Skagerrak (100-509 m depth) during a survey in the summer of 2006. Four species are new and formally described here. *Espegrendia norvegica* Westblad, 1954, (Solenopharyngidae), previously only known from its type locality, is redescribed. For the sake of completeness, two more undetermined species are mentioned, which brings the total number of species to 15. Additional remarks are given for all known species.

Materials and methods

During two sampling campaigns (30 May–8 June and 22–29 August 2006) both macro- and meiofauna of the deeper parts of Skagerrak were collected. Locality data are given in Table 1.

TABLE I. Overview of sites where rhabdocoels were collected. (Ws: Waren dredge; Az: Agassiz trawl).

Locality	Dredge type	Date	Bottom type	Start Lat	Long	**Stop** Lat	Long	**Min depth (in m)**	**Max depth (in m)**
Loc. 1	Ws	2006-05-31	mud	58º41’18’’E	10º50’42’’N	58º41’45’’E	10º51’28’’N	116	161
Loc. 2	Ws	2006-06-05	loamy mud	58º21’00’’E	10º27’39’’N	58º21’24’’E	10º28’22’’N	331	353
Loc. 3	Az	2006-06-05	mud	58º21’17’’E	10º27’35’’N	58º20’51’’E	10º27’19’’N	302	373
Loc. 4	Ws	2006-06-06	mud and gravel	58º29’00’’E	10º08’23’’N	58º28’21’’E	10º07’39’’N	500	509
Loc. 5	Az	2006-06-06	loamy mud	58º26’54’’E	10º13’40’’N	58º26’44’’E	10º14’23’’N	434	471
Loc. 6	Ws	2006-08-22	mud	58º17’06’’E	10º28’57’’N	58º17’27’’E	10º28’41’’N	335	395
Loc. 7	Ws	2006-08-23	mud	57º56’13’’E	11º13’52’’N	57º55’43’’E	11º14’14’’N	100	102

Sediment was obtained using an Agassiz trawl or a Warén dredge, whereafter the sediment was kept in large plastic boxes. The boxes were further filled with sea-water, turning over the sediment, and left in the dark at a constant temperature (± 15 ºC). After settling of the sediment (= 10 hours), the water just above it was carefully siphoned off and filtered through a sieve (mesh width: 125 µm).

Collected specimens were studied alive using a dissecting and a light-microscope. Whole-mounts were prepared using lactophenol. Specimens for histology were fixed in hot marine Bouin’s solution, embedded in paraffin and serially-sectioned. The sections (4 µm thick) were stained with Heidenhain’s iron haematoxylin, and erythrosine.

Specimens of *Pterastericola psilastericola* (Jespersen & Luetzen, 1972) Jondelius, 1992 were collected from a single specimen of the starfish *Psilaster andromeda* (Müller & Troschel).

Freehand drawings of live individuals were made using both dissecting and compound microscope. Drawings of hard parts (stylets, bursal appendages and proboscis hooks) were made using a camera lucida and accompanied by a scale bar. Measurements of these structures were made axially unless otherwise indicated. Positions of organs are expressed in percentages of the total body length. Live specimens were photographed using a compound microscope.

All material including types will be deposited in the collections of the Swedish Museum of Natural History (Stockholm). For several of the mentioned species, material (including types) present at the SMNH was studied for comparison.

Abbreviations used in the figures

b, brain; **bc,** copulatory bursa; **bst,** bursal stalk; **bu,** bursa (1-2, explained in text); **cga,** common genital atrium; **ci,** cirrus; **cil,** cilia (of distal pharyngeal rim); **cm,** circular muscle layer; **de,** ejaculatory duct; **div**, diverticle; **e,** eye; **ecm,** external circular muscle layer; **egg,** extracapsular prostate glands; **elm,** external longitudinal muscle layer; **ep,** epithelium (1-3, explained in text); **evs**, external seminal vesicle; **fg,** female glands; **gm,** glands of Minot; **gp,** gonopore; **h,** proboscis hook; **i,** intestine; **icm,** internal circular muscle layer; **igg,** intracapsular prostate glands; **ilm,** internal longitudinal muscle layer (1-2, explained in text); **ivs,** intracapsular seminal vesicle; **lm,** longitudinal muscles; **m,** mouth; **ma,** male atrium; **mgs,** male genital system; **od,** oviduct; **ov,** ovary; **p,** proboscis; **pc,** prepharyngeal cavity; **pg,** pharyngeal glands (1-3, explained in text); **ph,** pharynx; **pl,** pharynx lumen; **ppt,** pharynx protractors; **pr,** proboscis retractors; **ptr,** protractors; **pv2,** prostate vesicle type 2; **rg,** rostral glands; **rm,** radial muscles; **rs,** seminal receptacle; **sph,** sphincter; **st,** stylet; **stII,** prostate stylet type II; **stIII,** prostate stylet type III; **t,** testis; **ut,** uterus; **vd,** vas deferens; **vit,** vitellarium; **vg,** prostate vesicle; **vs,** seminal vesicle; **x-y,** explained in text.

Taxonomic results

Although a recent phylogenetic analysis of the Rhabdocoela exists (Willems *et al.* 2006a), the taxonomy of the group is still in need of revision, because the analysis showed a slight sampling bias towards marine species, nor did it include representatives of all subtaxa. Therefore species are organised alphabetically into four different categories: new species, redescribed species, new records and unidentified species. An overview of species following traditional taxonomy at the family-level, but reflecting the phylogeny by Willems et al. (2006a) at the higher-taxon-level, is given in Table 2.

TABLE 2. Complete species list with indication of new species for Sweden.

Rhabdocoela		**New to Sweden**
Kalyptorhynchia	**Acrumenidae**	
	Acrumena spec.	*
	Gnathorhynchidae	
	Prognathorhynchus dubius	
	Uncinorhynchus vorago **sp. nov.**	*
	Koinocystididae	
	Utelga heinckei	
	Placorhynchidae	
	Placorhynchus echinulatus	
	Polycystididae	
	Austrorhynchus artoisi **sp. nov.**	*
	Mesorhynchus terminostylus	

……continued on the next page

TABLE 2 (continued)

Rhabdocoela		New to Sweden
Dalytyphloplanida	**Pterastericolidae**	
	Pterastericola psilastericola	*
	Solenopharyngidae	
	Anthopharynx vaginatus	
	Espegrendia norvegica	*
	Lenopharynx bathos **sp. nov.**	*
	Proceropharynx profundum **sp. nov.**	*
	Trisaccopharynx westbladi	
	Trigonostomidae	
	Ceratopera spec.	*
	Proxenetes segmentatus	*

New species

***Austrorhynchus artoisi* sp. nov.**
(Fig. 1A–C)

Localities. Loc. 2 and Loc. 4 (type locality).

Material. Three individuals studied alive. Two whole mounts (one from each locality), one of them designated holotype (SMNH no. 7175). One serially-sectioned specimen (designated paratype; SMNH no. 7176).

Etymology. Species dedicated to Prof. Dr Tom Artois (Hasselt University) for his contributions on polycystidid taxonomy and systematics, and for being a close friend and colleague to Ulf Jondelius and Wim Willems.

Description. The animals are 0,9–1,4 mm long (measured on whole mounts), white to greyish, rather opaque and have no eyes. In all live individuals an almost round, bright yellow-orange egg (Fig. 1A: x) was present (dimensions: 304 x 342 µm). The general organisation in the live animals (Fig. 1A) is identical to that of other species of *Austrorhynchus* Karling, 1952a. In one of the live individuals four pairs of proboscis retractors (Fig. 1A: pr) could clearly be seen, whereas testes were not visible in the studied specimens.
The only serially-sectioned individual is in bad shape, because the presence of an egg caused rupture of the central part of all sections. Quality is however sufficient to study the general structure of the proboscis, pharynx and the genital system, which is comparable to that in other species of *Austrorhynchus* (see Karling 1952a; Artois & Schockaert 2003, 2005). The main differences with the other 16 known species of *Austrorhynchus* are found in the detailed structure of the two hard parts in the male genital system: prostate stylets type II and III (terminology of Artois & Schockaert 2003).

The double-walled prostate stylet type II (Fig. 1A: stII, 1B) is 61–63 µm (n = 2, as for all following measurements for this species) long and consists of a very short proximal funnel and a distal tube (4 µm wide), of which the tip is slightly bent. The funnel-shaped part is 20,5–24 µm wide and its length is approximately 1/7 of the total length. The inner stylet is not restricted to the distal part of the outer stylet and even bulges out of the funnel proximally. The outer stylet does not carry any spines or hooks, but the funnel-shaped part is ornamented with a ring, which gives the proximal part of the stylet the shape of a stirrup. It is 28–31 µm wide and 21–28 µm long. The prostate stylet type III (Fig. 1A: stIII, 1C; A-organ in Karling 1977) closely resembles that of *A. hawaiiensis* Karling, 1977. The style and foot, which are 42–54 µm apart, are clearly recognisable,

but unpronounced. They are interconnected by a narrow clasp (terminology of Willems et al., 2006b) and a thin, comb-bearing plate, which is 21 µm at its broadest point. The clasp is strongly bent and situated very close to the thickened, proximal edge of the plate, giving the whole the appearance of an eight-shaped ring. The inconspicuous foot is situated at the base of a thread-like flagellum, which is 86–90 µm long (measured from the proximal rim of the foot). This flagellum shows a strong curve at ± 65% of its length, but does not bear a comb nor is its distal end swollen. The most proximal third of the flagellum is not free, but connected to the plate.

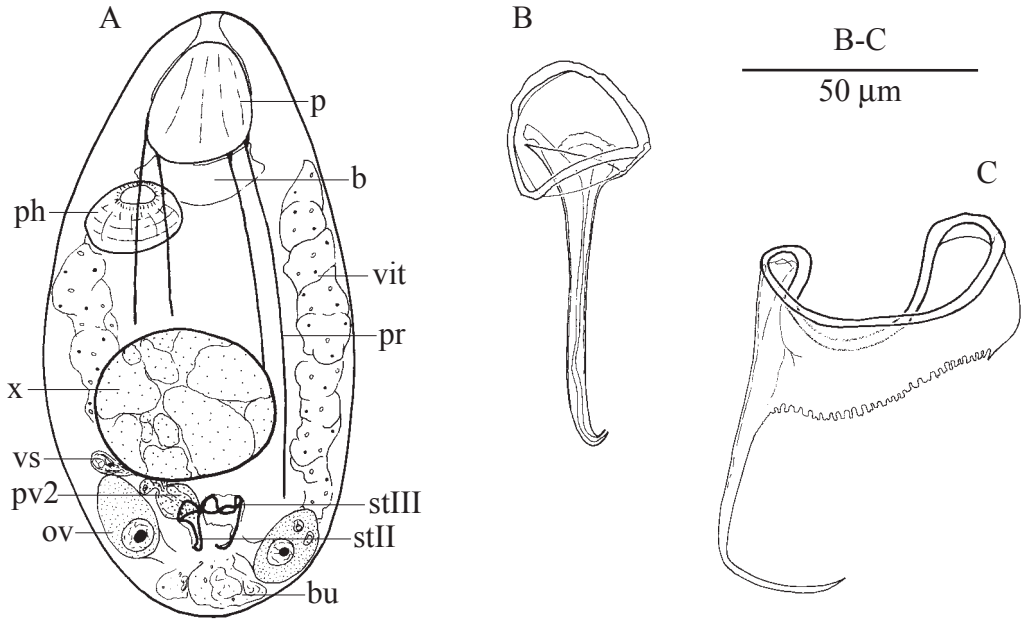

FIGURE 1. *Austrorhynchus artoisi* **nov. sp.** A, general organisation (from a live individual). B, prostate stylet type II (from the holotype). C, prostate stylet type III (from the holotype).

Diagnosis. *Austrorhynchus artoisi* **sp. nov.**: species of *Austrorhynchus* without eyes; double-walled stylet type II ca. 62 µm, consisting of a short proximal funnel, approximately 1/7 of the total length, and a distal tube with a bent tip; inner stylet is not restricted to distal part of outer stylet, which only carries a stirrup-shaped ornament proximally; stylet type III shows an unpronounced foot and stylet, ca. 48 µm apart; the foot tapers into a thread-like flagellum, which is ca. 88 µm long, bent and connected to a thin, comb-bearing plate.

Discussion. Within the taxon *Austrorhynchus*, the 16 hitherto known species mainly differ in the detailed structure of the two prostate stylets. In *A. artoisi* **sp. nov.** both stylets show a combination of features, not present in any other species of *Austrorhynchus*. The stylet type II of *A. artoisi* has a very short funnel-shaped part, approximately 1/7 of the total stylet length. Only in *A. karlingi* Brunet, 1965 and *A. scoparius* Brunet, 1965 the basal tube is similarly short. The total length of the stylet is significantly larger (100–110 µm in *A. karlingi* and 80–100 µm in *A. scoparius*; see Brunet 1965). In most species of *Austrorhynchus* the stylet type II bears a hook, which is absent in *A. artoisi* and five more species (*A. antarcticus* Artois *et al*., 2000, *A. galapagoensis* Artois & Schockaert, 1999, *A. pacificus* Karling, 1977, *A. pectatus* Karling, 1952a and *A. scoparius*; see Karling 1952a, 1977; Brunet 1965; Artois & Schockaert 1999; Artois *et al*. 2000). Besides in *A. artoisi*, a distally bent stylet tube is only found in *A. calcareus* Karling, 1977 (see Karling 1952a, 1977). Two features regarding the stylet type II are clearly unique for *A. artoisi*: presence of a stirrup-shaped ornament and the inner stylet that is as long as the outer stylet. Whereas type II stylets are rather simple in structure, stylets of type III are more complex, and especially in species of *Austrorhynchus* they show a great variety in shape and size. Apart from the one present in *A. artoisi*, there are only four species of *Austrorhynchus* with an annular type III stylet: *A. californicus* Karling, 1977*, A galapagoensis*, *A. hawaiiensis* and *A. pacificus* (see

Karling 1977; Artois & Schockaert 1999; Willems *et al*. 2006). Of these *A. galapagoensis* clearly has an aberrant stylet, whereas in the other three the clasp (terminology of Willems *et al.* 2006) is not situated close to the plate, as is the case in *A. artoisi*. The reason for this is the presence of a more pronounced foot, in comparison with the situation in *A. artoisi*.

Apart from the hard structures in the male genital system, there is yet another interesting feature distinguishing *A. artoisi* from most other species of *Austrorhynchus*, namely the absence of eyes. Besides in *A. artoisi*, they are only lacking in four other species: *A. antarcticus*, *A. karlingi* Brunet, 1965, *A. magnificoides* Artois *et al*., 2000 and *A. magnificus* Karling, 1952a (see Karling 1952a, 1977; Brunet 1965; Artois *et al.* 2000).

This is the first record of a species of *Austrorhynchus* from the northern Atlantic region, and thus fills in the gap mentioned by Karling (1977: p. 159 and Fig. 9). Apart from the Mediterranean species (*A. bruneti* Karling, 1977, *A. karlingi* and *A. scoparius*), this is the only species of the taxon occurring in European waters. Most species of *Austrorhynchus* have a very limited distribution, in most cases they are only known from one locality. An exception is *A. hawaiiensis*, found on Hawaii, the East-African coast and the eastern Australian coast (Karling *et al*. 1972; Karling 1977; Willems *et al.* 2006b)

***Lenopharynx bathos* sp. nov.**
(Fig. 2A–D)

Locality. Loc. 4 (type locality).

Material. One animal studied alive and serially-sectioned (designated holotype; SMNH no. 7177).

Etymology. Species name refers to the depth of which the animal was collected. Bathos (Greek): the depth of the sea, the deep.

Description. The almost globular animal (Fig. 2C) is very small but could not be measured exactly. It is colourless and lacks eyes. The epidermis is 0,4 µm thick and carries 0,3 µm long cilia.

The pharynx (Fig. 2D) is extremely long and slender and therefore has a snake-like appearance in live individuals. It is found in the rostral half of the body, with the mouth at approximately 70 %. No details regarding the mouth opening or the connection with the prepharyngeal cavity could be observed, because of damage to the ventral side of the body in the single serially-sectioned individual. The prepharyngeal cavity (Fig. 2D: pc) is very deep (± 30 % of the pharynx length), lined with a very high, nucleated epithelium and surrounded by strong longitudinal muscles that act as pharynx protractors (Fig. 2D: ppt). A circular muscle layer could not be discerned. The distal pharyngeal rim bears no cilia. The pharynx proper is surrounded by inner circular (Fig. 2D: ecm) and outer longitudinal muscles (Fig. 2D: elm). Internal musculature of the pharynx consists of radial muscles (Fig. 2D: rm), a very weak longitudinal muscle layer (Fig. 2D: ilm) and circular muscles (Fig. 2D: icm). The exact numbers of these muscles could not be determined. At the distal end of the pharynx the internal circular muscles are stronger, forming a sphincter. The pharynx lumen (Fig. 2D: pl) is lined with a high, frayed and anucleated epithelium. The pharynx contains two types of glands: one fine-grained, eosinophilic and one fine-grained basophilic type both of which have an extra-pharyngeal part and enter the pharynx proximally. Both gland-types open near the distal end. About midbody, ventrally from the pharynx but not associated with it, a large bundle of both eosinophilic and basophilic glands is present.

The common genital pore (Fig. 2B: gp) is situated at approximately 80%, just behind the mouth. It opens into a wide genital atrium (Fig. 2B: cga) that receives the male system rostrally and the female system dorsally. The common genital atrium is surrounded by inner circular and outer longitudinal muscles and lined with a very low, anucleated epithelium. The circular muscle layer is very weak proximally. A vaguely delineated bursa (Fig. 2B: bu) is situated caudodorsally of the genital atrium and opens into it through a short, muscular stalk (Fig. 2B: bst). The male atrium (Fig. 2B: ma) is surrounded by inner circular and outer longitudinal

muscles and lined with a high, nucleated epithelium. The copulatory bulb proper is almost globular in shape and surrounded by inner circular and outer longitudinal muscles. The circular muscle layer is very thin and inconspicuous proximally and becomes gradually thicker distally. Before entering the copulatory bulb, both swollen and winding vasa deferentia (Fig. 2B: vd) fuse, forming a short seminal duct. This duct, which can be closed by a strong sphincter, enters the copulatory bulb together with a bundle of course-grained basophilic glands and forms an internal seminal vesicle (Fig. 4B: ivs). This vesicle opens into a separate compartment of the copulatory organ, together with fine-grained eosinophilic and course- and fine-grained basophilic prostate glands (Fig. 4B: igg). This compartment is surrounded by weak circular muscles proximally and opens into the stylet that is associated with the copulatory bulb. The simple, straight stylet (Fig. 2A, 2B: st) is slightly wider proximally and has a rounded distal tip. It is approximately 75 µm long (measured on a live individual).

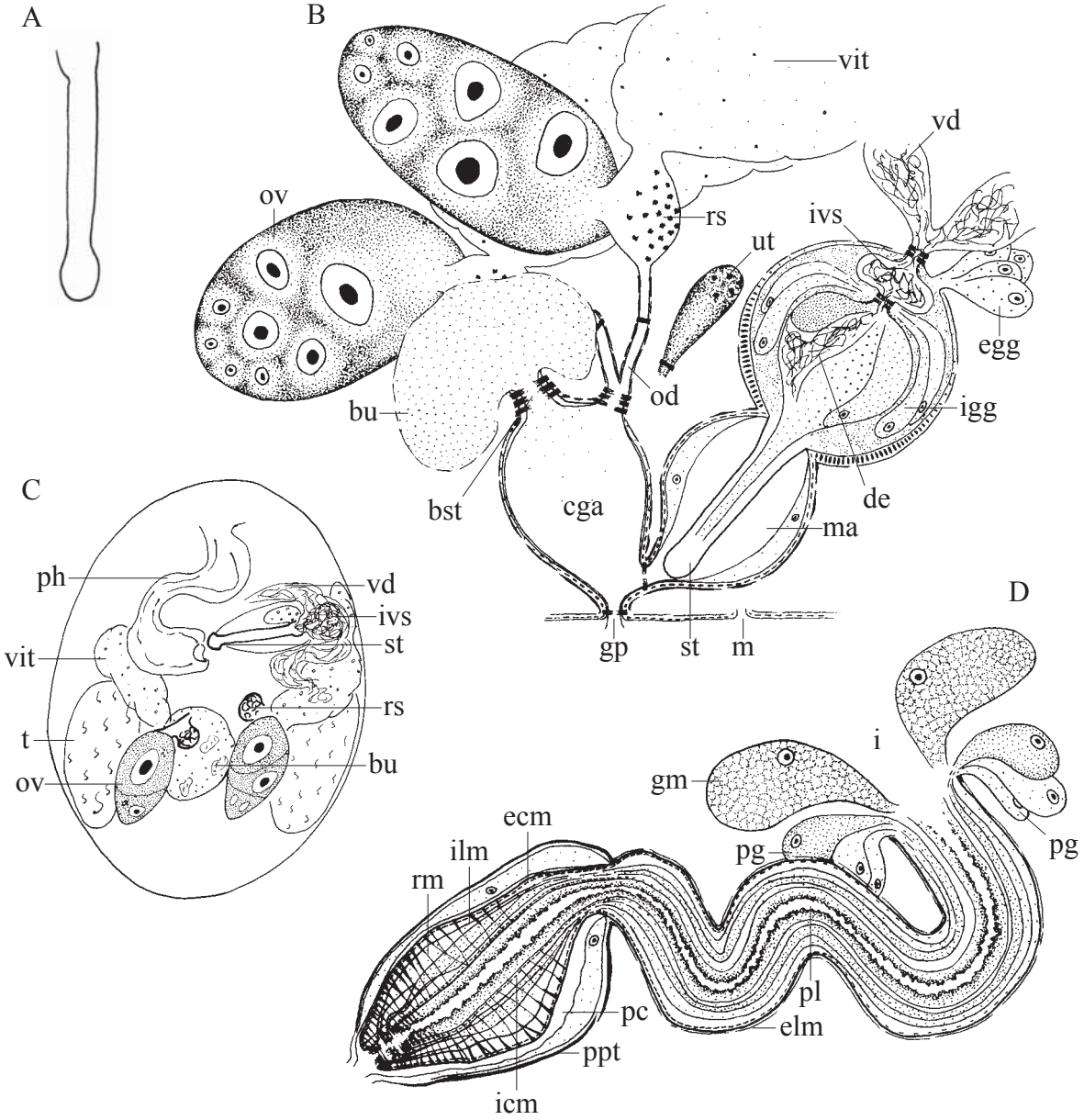

FIGURE 2. *Lenopharynx bathos* **nov. sp.** A, stylet (from a live individual; freehand drawing). B, reconstruction of the atrial organs from the right side (from the holotype; radial muscles in proximal part not shown for reasons of clarity). C, general organisation (from a live individual). D, reconstruction of the pharynx from the right side (from the holotype).

The paired, caudally situated ovaries (Fig. 2B: ov) are oval in shape and each of them is connected to a swollen, sperm-filled seminal receptacle (Fig. 2B: rs). The almost globular vitellaria (Fig. 2B: vit) are connected to the seminal receptacles through separate wide vitelloducts that enter the receptacles dorsally. The narrow oviducts (Fig. 2B: od) are surrounded by weak longitudinal muscles and leave the seminal receptacles ventrally. A sphincter is present near the middle of the oviducts, which fuse into a very short female duct. This duct enters the common genital atrium dorsally, where it can be closed by a very strong sphincter. A uterus (Fig. 2B: ut) is present but its connection to the genital atrium could not be discerned.

Diagnosis. *Lenopharynx bathos* **sp. nov.**: colourless species of *Lenopharynx* without eyes and with a straight, tubular stylet, which is ca. 75 µm long, widened proximally and has a rounded distal tip.

Discussion. This species clearly is a member of Solenopharyngidae Graff, 1882, as it shows the following diagnostic features: ventrocaudally-oriented, elongated pharynx, strongly-developed extrapharyngeal glands, a caudally-situated mouth, presence of a common genital pore, paired testes, intracapsular prostate glands and paired vitellaria (see Ehlers 1972).

This species closely resembles species of the taxon *Lenopharynx* Beklemischev, 1929 in the overall organisation of the genital system. This taxon includes three species: *L. languidus* Beklemischev, 1929, *L. triops* Marcus, 1951 and *L. tubatus* Schockaert & Martens, 1985, which are all characterized by the presence of a long snake-like pharynx, a bursa with a highly muscular bursal stalk, paired ovaries, two seminal receptacles and a male copulatory organ with an internal seminal vesicle.

Unlike *L. languidus* and *L. triops*, both species with an armed cirrus (see Marcus 1951; Beklemischev 1929; Ehlers 1972), *L. tubatus* and *L. bathos* are characterised by the presence of a simple, tubular stylet. However, the stylet differs in shape between the latter two species. In *L. tubatus* it is not widened proximally and it has a straight distal edge, whereas the stylet of *L. bathos* is wider proximally (almost cup-shaped) and has a rounded distal tip. Unfortunately, their lengths cannot be compared, as the stylet is not preserved in the holotype of *L. tubatus* (see Schockaert & Martens 1985). Other differences between the two species are the presence of eyes and blackish-brown colouration found in *L. tubatus* but missing in *L. bathos,* which is colourless, transparent and lacks eyes.

***Proceropharynx profundum* sp. nov.**
(Fig. 3A–D)

Localities. Loc. 2 and Loc. 5 (type locality).

Material. Three animals studied alive. One whole-mounted specimen and two serially-sectioned individuals, one of them designated holotype (SMNH no. 7178), the other one paratype (SMNH no. 7179).

Etymology. Species name refers to the depth at which the animal was found and the fact that, until now, very few rhabdocoels were collected from such deep localities. Profundum (Latin): the depth, the abyss.

Description. The relatively small animal is yellow and lacks eyes. The cellular epidermis is 0,6–0,8 µm thick with ± 0,4 µm long cilia.

The pharynx (Fig. 3A) is elongated and situated midbody with the mouth at ± 80 % (measured on sections). The prepharyngeal cavity (Fig. 3A: pc) is very narrow and lined with a nucleated epithelium. The distal part of the prepharyngeal cavity is tubular and can be closed by a weak sphincter, which is situated close to the mouth. Longitudinal muscles surround both the prepharyngeal cavity and the duct connecting it with the mouth. The external pharyngeal muscles consist of a weak, outer longitudinal (Fig. 3A: elm) and an inner circular muscle layer (Fig. 3A: ecm). Internal radial, circular and very weak longitudinal muscles (Fig. 3A: rm; icm; ilm) are present but their exact numbers could not be determined. Three types of pharyngeal glands, one of fine-grained, eosinophilic type and two of fine-grained (slightly different in grain-size), basophilic type enter the distal part of the pharynx. They all have a large extra-capsular part and enter the pharynx at its prox-

imal end. Fine-grained eosinophilic glands (not indicated on Fig. 3A for reasons of clarity) surrounded by strong longitudinal muscles are situated around the distal part of the pharynx bulb. It is unclear whether or not they enter the pharynx.

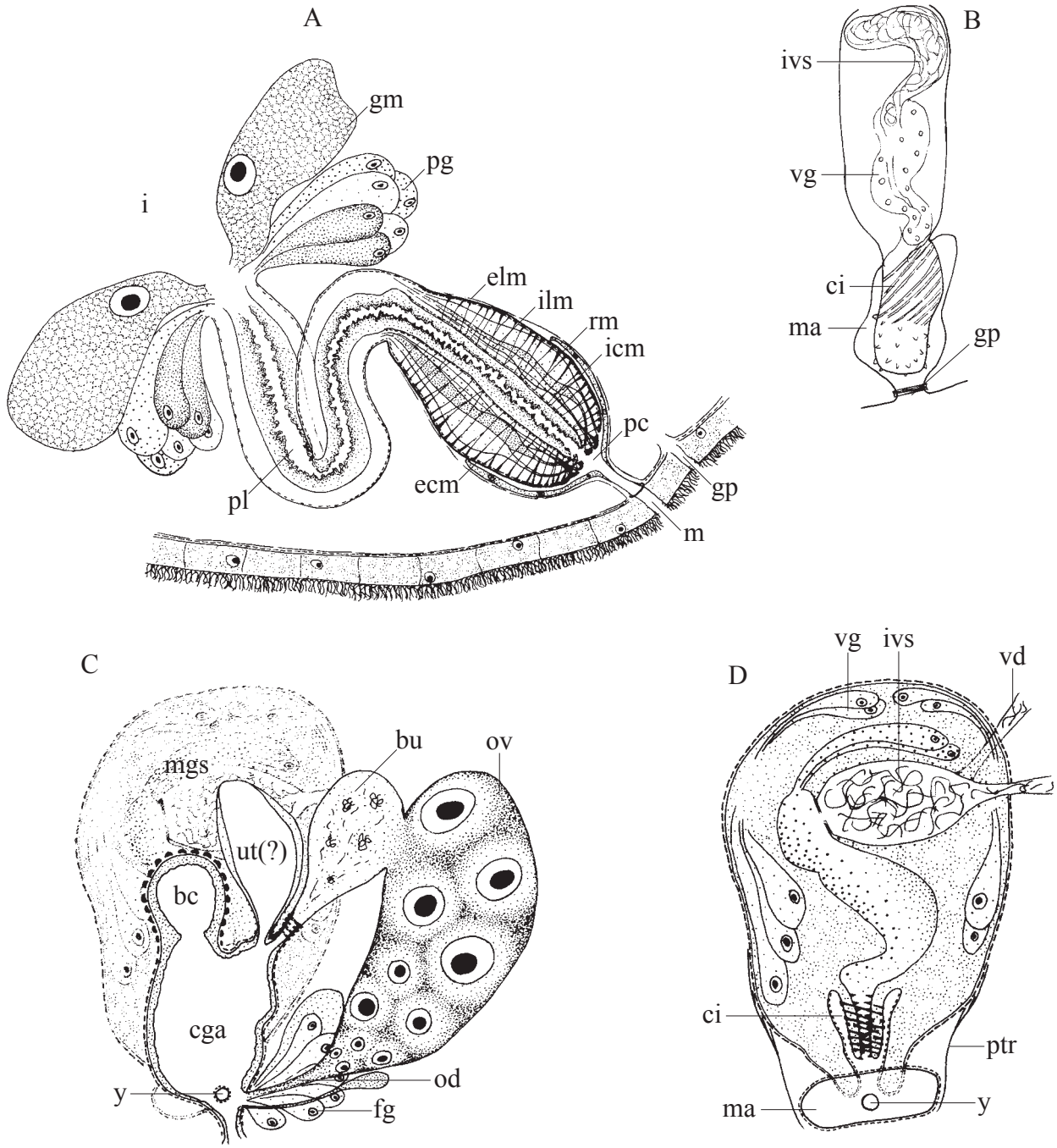

FIGURE 3. *Proceropharynx profundum* **nov. sp.** A, reconstruction of the pharynx from the right side (from the holotype; radial muscles and gland necks in proximal part not shown for reasons of clarity). B, copulatory organ (from a live individual). C, reconstruction of the atrial organs from the right side (from the holotype). D, reconstruction of the male genital system (from the holotype).

The gonopore (Fig. 3A: gp) is situated just behind the mouth in the most caudal part of the animal. Both the mouth and the gonopore lie very close together, but are not associated with each other. The gonopore leads to the common genital atrium (Fig. 3C: cga) which is lined with a high anucleated epithelium and surrounded by circular muscles. At the dorsal side of the genital atrium a more or less separate compartment (Fig. 3C: bc) is present. This so-called copulatory bursa (terminology of Ehlers 1972) is surrounded by a very strong circular muscle layer and lined with a high anucleated epithelium. Dorsocaudally an empty vesicle that could be the uterus (Fig. 3C: ut?), lined with a low anucleated epithelium and a resorptive bursa (cf. seminal bursa of Ehlers, 1972; Fig. 3C: bu) enter the genital atrium very close to one another. The bursa is filled with sperm in different stages of resorption and both the bursa and the empty vesicle are distally surrounded by circular muscles. The genital atrium receives the male atrium ventrocaudally (through y on Fig. 3C). A single oviduct enters the atrium from the caudal side.

The two testes are situated ventrocaudally and are not interconnected. The short vasa deferentia (Fig. 3D: vd) enter the male copulatory organ separately and lead into an internal seminal vesicle (Fig. 3B & D: ivs). This vesicle is surrounded by weak circular muscles. The globular copulatory organ and the small male atrium (Fig. 3B & C: ma) are surrounded by strong circular and weaker longitudinal muscles. The internal seminal vesicle opens into a compartment filled with course-grained, basophilic and fine-grained, eosinophilic secretion. The basophilic secretion is produced by glands in the upper part of the male organ. Fine-grained basophilic glands fill the rest of the male bulb. The distal part of the male organ consists of a long cirrus (Fig. 3B & D: ci) with small spines distally and hard ridges proximally (clearly seen on the live individual). In the sectioned material the cirrus is partially retracted, resulting in the spiny section being inverted into the section with ridges (see Fig. 3D: ci)

The single, large ovary (Fig. 3C: ov) is situated caudally and connected with the common genital atrium through a short and narrow oviduct (Fig. 3C: od). The proximal part of the ovary and the resorptive bursa lie close together and are associated with each other through a broad and indistinct connection.

A large bundle of fine-grained, eosinophilic and fine-grained, basophilic glands (Fig. 3C: fg) open into the genital atrium, together with the oviduct. Vitellaria and vitelloducts could not be discovered.

Diagnosis. *Proceropharynx profundum* **sp. nov.**: species of *Proceropharynx* with a cirrus with small spines distally and ridges proximally; copulatory bursa small without hard structures.

Discussion. *Proceropharynx profundum* **sp. nov.** clearly is a member of the taxon Solenopharyngidae Graff, 1882, and shows all diagnostic features of the taxon (see diagnosis in discussion of *Lenopharynx bathos* **sp. nov.**). Within the Solenopharyngidae the combination of a long ejaculatory duct with ridges and a very muscular copulatory bursa is only found within the taxon *Proceropharynx* Ehlers, 1972. This taxon contains *P. litoralis* Ehlers, 1972 and *P. anophthalmus* Ehlers, 1972, which have the same general organisation as *P. profundum* **sp. nov.** These two species are however colourless, have inter-connected rostrally-situated testes and ridges or lamellae on the cirrus. The presence of both hard ridges (on the proximal part of the cirrus) and small spines (on the distal part of the cirrus) is unique within the Solenopharyngidae.

***Uncinorhynchus vorago* sp. nov.**
(Fig. 4A–C)

Type locality. Loc. 2.

Type material. One animal studied alive, whole-mounted and designated holotype (SMNH no. 7180).

Etymology. Species name refers to the type locality. Vorago (Latin): of watery depths, an abyss, chasm.

Description. The live animal was only observed for a short time, both because of its initial preliminary identification as *Uncinorhynchus flavidus* Karling, 1947, and a high degree of squashing early on. Therefore the exact location of the pharynx and the presence and structure of the organs could not be determined.

The rather slender animal is yellow and lacks eyes. The two proboscis hooks (Fig. 4A) are 29 µm high (top-bottom measurement), each with two, 51 µm-long basal wings and a curved pointed hook. At the transition between the actual hook and the wings, a very thin, frayed hem is present. The pear-shaped to globular, very muscular prostate vesicle (Fig. 4C) is situated in the most caudal part, receives sperm from a simple, large and extracapsular seminal vesicle (Fig. 4C: vs) and is connected to a triangular stylet (Fig. 4B, 4C: st). The stylet (Fig. 4B), which has a rather blunt and short distal tip, is 76 µm long and consists of one big plate that is folded into two halves along the convex side of the structure and forms a tube distally. One of the halves shows a lot of wrinkles and folds and the other is rather large and gutter-shaped.

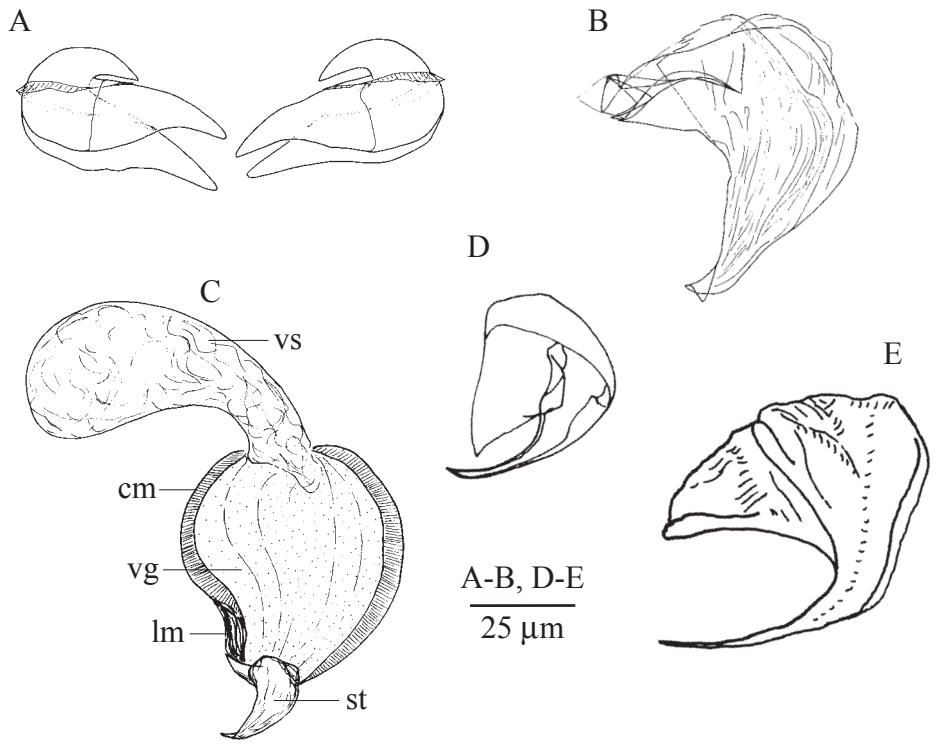

FIGURE 4. *Uncinorhynchus vorago* **nov. sp.** A, proboscis hooks (from a whole-mount). B, stylet (from a whole-mount). C, copulatory organ (from a live individual). *Uncinorhynchus flavidus* D, stylet (from South Georgia; SMNH no. 53053). E, stylet (from Finland; after Karling, 1947).

Diagnosis. *Uncinorhynchus vorago* **sp. nov.**: species of *Uncinorhynchus* with yellow colour and lacking eyes; proboscis hooks ca 29 µm high with basal wings ca. 51 µm long and curved pointed hook; triangular stylet ca. 76 µm long with blunt distal tip, consisting of folded plate which has a tubular part distally.

Discussion. The taxon *Uncinorhyncus* Karling, 1947 includes 6 species which are all marine, except for *U. karlingi* Kolasa, 1977, a freshwater species. All species are characterised by the presence of proboscis hooks with two long basal wings and a hook-shaped stylet. The shape of the stylet is very variable, but in known species it always shows a rather long, in some species needle-shaped, in others more dagger-shaped distal tip (Karling 1947, 1952b, 1989; Brunet 1973; Kolasa 1977). Especially the stylet of *U. flavidus* (Fig. 4D–E) is superficially similar to that of *U. vorago*, both in general shape and size (Karling 1947, 1952a, 1989), but in *U. vorago*, the needle-shaped distal tip is lacking. *Uncinorhynchus vorago and U. flavidus* both occur in Skagerrak and have a yellow body colour (see Karling 1974).

Redescription

***Espegrendia norvegica* Westblad, 1954**
(Fig. 5A–B)

Localities. Loc. 1, Loc. 4 and Loc. 5.

Known distribution. Northern Atlantic, Norway (Westblad 1954).

Material. A few individuals from Skagerrak studied alive, three of them serially-sectioned. Three serially-sectioned individuals from a depth between 50 and 100 m at Skipelle near Drøbak, Norway (18/08/1955; coll. Westblad, SMNH nos 32853–32855).

Description and remarks. Up till now this species is only known from one cross-sectioned specimen (designated holotype), described by Westblad (1954). As already pointed out by Ehlers (1972), the original description is unsatisfactory and especially the detailed organisation of the male system as described and depicted by Westblad (1954) is highly doubtful. This is probably caused by the nature of the holotype as the interpretation of cross-sections is often very hard, especially regarding long and winding structures as a cirrus. A redescription is therefore deemed necessary.

The following redescription is based on the newly collected material from Skaggerak and sectioned specimens collected by Westblad in Norway (August 1955), which were never reported upon.

The Skagerrak specimens are rather small and colourless and lack eyes. They have a drop-shaped, slightly elongated body if swimming freely, but are oval-shaped or almost round when immobilized. The syncytial epidermis is 3–4 μm thick, contains small rod-shaped rhabdites, equally distributed over the entire epidermis, and is covered with short cilia that are of equal length over the whole body. The outer circular muscles of the subepidermal body wall musculature (Fig. 5A: cm) are exceptionally thick, whereas the inner longitudinal muscles (Fig. 5A: lm) are rather weak.

The pharynx (Fig. 5A) is situated in the first body half. It is oriented caudally and can be fairly long (maximally half of the total body length), almost snake-like, altough it can strongly vary in length, depending on the degree of contraction. A separate mouth is lacking, as the prepharyngeal cavity is connected to the genital atrium through a short duct, which is lined with a low, nucleated epithelium and surrounded by longitudinal muscles. The prepharyngeal cavity proper (Fig. 5A–B: pc) is very deep, lined with a low, anucleated epithelium and surrounded by longitudinal muscles (Fig. 5A: ep1). The distal pharyngeal rim bears short cilia (Fig. 5A: cil) and the pharynx bulb, bulging out into the prepharyngeal cavity is covered with the remains of a degenerated epithelium (Fig. 5A: ep2). The pharynx lumen (Fig. 5A: pl) is almost completely filled by a degenerated epithelium (= pseudociliation; Fig. 5A: ep3). The pharynx is surrounded by an outer longitudinal (= continuation of layer surrounding the prepharyngeal cavity; Fig. 5A: elm) and an inner circular muscle layer (Fig. 5A: ecm). The internal muscles consist of rather weak radial muscles (Fig. 5A: rm), a circular (Fig. 5A: icm) and two longitudinal (Fig. 5A: ilm1–2) muscles layers. The longitudinal layer immediately surrounding the pharynx lumen (Fig. 5A: ilm1) consists of eight thick muscle fibers, whereas the second layer ((Fig. 5A: ilm2), situated more peripherically consists of at least 30 weaker fibers. Two types of glands enter the pharynx proximally (Fig. 5A: pg1–2). One type of glands is rather small and contains a fine-grained eosinophilic secretion (Fig. 5A: pg1), whereas the second type consists of very large gland cells, containing a basophilic rod-shaped secretion (Fig. 5A: pg2). A few glands of the latter type are also present intracapsulary (Fig. 5A: pg3). The exact location where these glands open into the lumen could not be determined.

The common genital pore, which is combined with the mouth (Fig. 5A–B: m + gp), is situated in the most distal part of the body. Close to this combined opening, the prepharyngeal cavity (Fig. 5A–B: pc) opens into the common genital atrium (Fig. 5A–B: cga) from the rostral side. The genital atrium is lined with a high nucleated epithelium and surrounded by inner circular and outer longitudinal muscles. The former are clearly thicker around the distal part of the genital atrium. The presence of nuclei is restricted to the most proximal

part of the atrium. A small, bean-shaped bursa (Fig. 5B: bu), which contains resorbed sperm, opens into the genital atrium from the dorsal side.

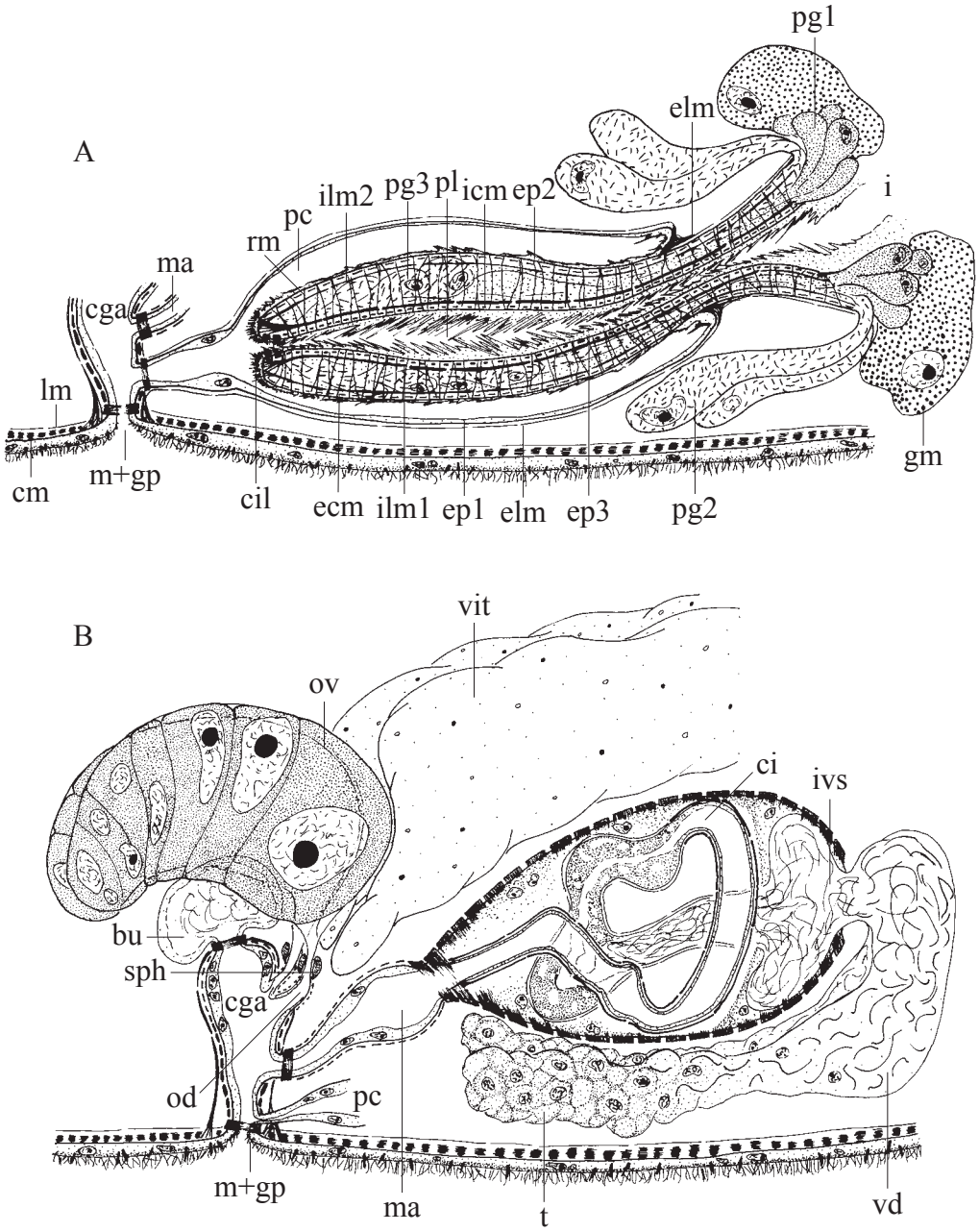

FIGURE 5. *Espegrendia norvegica* Westblad, 1954. A, reconstruction of the pharynx from the right side. B, reconstruction of the atrial organs from the right side. (A–B, from a Skagerrak-specimen).

Dorsally from the prepharyngeal cavity the male atrium (Fig. 5A–B: ma) opens into the genital atrium from the rostral side. The male atrium is a wide cavity proximally, distally narrowing to a duct. It is lined with a nuclated epithelium and surrounded by circular muscles. Proximally the male atrium is connected to the oval-shaped copulatory organ, which is surrounded by a very strong circular muscle layer and divided into two compartments. The most proximal part contains an internal seminal vesicle (Fig. 5B: ivs), which receives sperm directly from the swollen vasa deferentia (Fig. 5B: vd). The distal part of the copulatory organ contains a long, winding cirrus (Fig. 5B: ci), which is surrounded by a strong longitudinal muscle layer. Proximally the unarmed cirrus is filled with sperm, wheras the middle part is lined with a thick, glandular epithelium (eosino-

philic). The distal part of the cirrus, approximately half of its total length, is lined with a low, anucleated epithelium.

The female genital system is rather simple and only consists of two kidney-shaped ovaries (Fig. 5B: ov), situated dorsally to the genital atrium, to which they are connected through two short oviducts (Fig. 5B: od). They open into the atrium separately and are distally surrounded by a circular muscle layer, which forms a very thick and distinct sphincter (Fig. 5B: sph) half way the oviducts. A uterus is lacking.

Apart from the detailed organisation of the copulatory organ, the overall structure of the genital system is identical to that described by Westblad (1954). The male copulatory organ in the holotype is decribed as consisting of "two twisted chitinous filaments or tubes" (Westblad 1954: p. 17). However, careful re-examination of the holotype shows only a single, but strongly winding cirrus, which is not lined with a pseudocuticularised epithelium, but with a low anucleated epithelium.

Diagnosis. *Espegrendia* Westblad, 1954: Lenopharynginae with combined mouth and gonopore; resorbing bursa opening into common genital atrium; copulatory organ an oval-shaped, muscular bulb containing a seminal vesicle proximally and a long, winding and unarmed cirrus distally; oviducts with distinct sphincter.

Type species: *Espegrendia norvegica* Westblad, 1954: Provisionally with the same diagnosis as the genus.

New records

***Anthopharynx vaginatus* Karling, 1940**

Locality. Loc. 6.

Known distribution. Baltic Sea (see Luther 1963 and references therein).

Material. One individual studied alive.

Description and remarks. The animal was identified based on observations of the live specimen. Photos were taken but were unfortunately of poor quality.

***Mesorhynchus terminostylus* Karling, 1956**

Localities. Loc. 1, Loc. 2 and Loc. 6.

Known distribution. Northern Atlantic (see Karling 1956 and references therein).

Material. Three individuals studied alive. Three whole mounts.

Description and remarks. The animals are 1,1–1,7 mm long (measured on whole mounts). Their stylets are slightly bent because of excessive squashing. The three individuals show a clear difference in stylet length. Two of them have a stylet that is 46–49 µm long, whereas the third one is 81 µm long. The latter measurement is aberrant and falls clearly out of the known range (35–46,6 µm in Karling 1956). Proximally, the funnel of the stylet is 19–26 µm wide (n = 3; m = 22).

Apart from shallow habitats, this species is previously also found off the Norwegian and Greenland coast at 300 m and 180 m respectively (see Karling 1956).

***Placorhynchus echinulatus* Karling, 1947**

Material. One individual studied alive and whole-mounted.

Locality. Loc. 6.

Known distribution. Northern Atlantic: Norway (Karling 1947), Skagerrak (Karling 1952b).

Description and remarks. The general organisation of the single collected individual corresponds well to

Karling's (1947) original description, although not all structures could be seen on the live specimen, which had ingested a nematode.

***Prognathorhynchus dubius* Meixner, 1929**
(Fig. 6A–B)

Locality. Loc. 7.

Known distribution. Northern Atlantic, Germany (Noldt 1989b).

Material. One individual studied alive.

Remarks. Unfortunately, no material of this species could be preserved. However, observations on a single live individual (see Fig. 6A) allowed a positive identification, mainly based on the structure of the proboscis teeth (Fig. 6B) and the stylet (see Ax 1952).

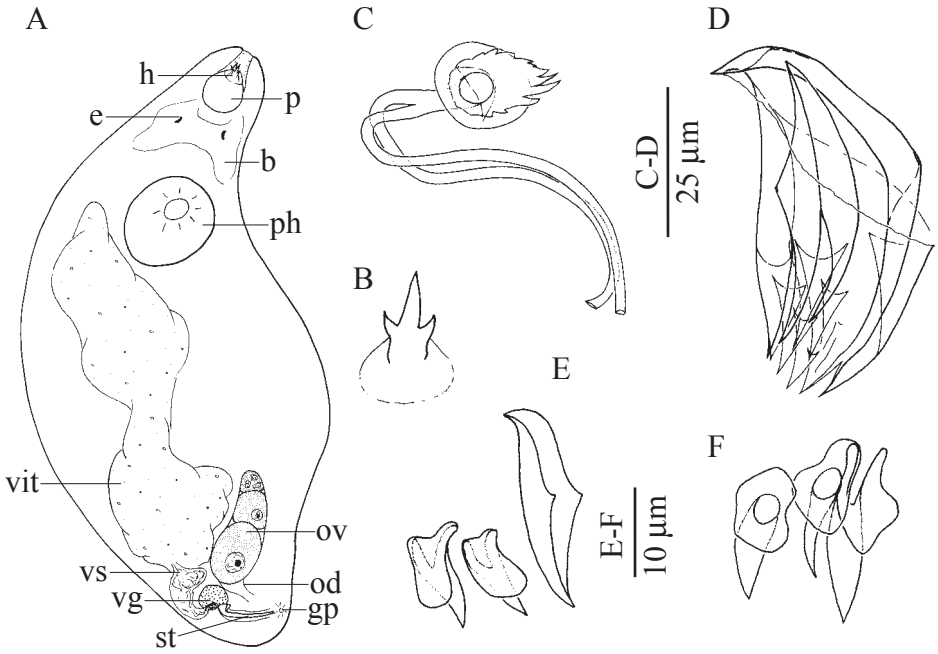

FIGURE 6. *Prognathorhynchus dubius* A, general organisation (from a live individual). B, proboscis hook (from live individual; freehand drawing). *Proxenetes segmentatus*. C, bursal appendage (from a whole-mount). D, stylet (from a whole-mount). *Utelga heinckei* E–F, stylet hooks of two different individuals (from whole mounts).

***Proxenetes segmentatus* Den Hartog, 1966**
(Fig. 6C–D)

Locality. Loc. 1.

Known distribution. Zeeland, Netherlands (Den Hartog 1966)

Material. One individual studied alive and whole-mounted.

Description and remarks. The plump, wide and open stylet (Fig. 6D) is 58 µm long. The curved, tubular part and the surrounding mantle, showing several spines are 83 µm and 35 µm long respectively. The ducts of the bursal appendage (Fig. 6C) are 86 µm long and the proximal cuticular ring is 17 µm wide. No other hard parts are present. The detailed structure and the size of both hard parts fits well with the description of *P. seg-*

mentatus Den Hartog, 1965. However, Den Hartog (1966) mentions a slightly shorter bursal appendage, 60 µm long.

This species was found by Den Hartog (1966) in a shallow salt-marsh, whereas our specimen was collected at a depth of 116–161 m.

***Pterastericola psilastericola* (Jespersen & Luetzen, 1972) Jondelius, 1992**

Locality. Loc. 3.

Known distribution. Northern Atlantic, Norway (Jespersen & Luetzen 1972).

Material. Four specimens studied alive and fixed in ethanol for future DNA extraction.

Description and remarks. No specimens were preserved as whole mounts but the identification is confirmed based on the presence of an ophistaptor, absence of ciliation over most of the body and the fact that it is the only species known to live as a symbiont in the pyloric caeca of the starfish *Psilaster andromeda* (see Jondelius 1992).

***Trisaccopharynx westbladi* Karling, 1940**

Localities. Loc. 2 and Loc. 6.

Known distribution. Northern Atlantic: Norway (Karling 1940).

Material. Two individuals studied alive and whole mounted (in poor condition).

Description and remarks. The specimens were identified based on observations on live material. The eye (= two eyes that are fused) is not visible in the preserved material. This was also observed earlier by Karling and explained as a result of the preservation method (pers. obs: info. on the label of a whole mount; see also Karling 1940).

***Utelga heinckei* (Attems, 1897) Karling, 1954**
(Fig. 6E–F)

Localities. Loc. 2 and Loc. 5.

Known distribution. Northern Atlantic (see Karling 1980 and references therein): west coast of USA, North Sea, Skagerrak, Irish Sea, Irish Atlantic coast.

Material. Two individuals studied alive and whole-mounted.

Description and remarks. In both studied individuals one of the three hooks associated with the male copulatory organ is larger than the two other ones (Fig. 6E: 23µm, 11µm, 11µm and Fig. 6F: 20µm, 11µm, 10µm). The measurements correspond to earlier data (e.g. Karling 1980: 22–36 µm), although the hooks are a bit shorter in the two Skagerrak-specimens. At first sight, the shape of the hooks seems to differ between the two individuals, but when closely examining their construction it is clear that they are all very similar. In both individuals all hooks have a straight gutter-shaped spine-like part and a more plate-like part that can be bent under different angles in respect to the spine-like part. This explains the overall difference in appearance between the hooks of both individuals, but also explains the odd shape of the larger hook in one individual (Fig. 6E), where the angle is ± 180º. In both specimens an odd-looking secretion consisting of light-refracting, very coarse grains is present in the prostate vesicle.

Unidentified species

***Acrumena* spec.**
(Fig. 7A–C, 8A)

Locality. Loc. 2.

Material. One individual studied alive.

Description. This description has to be viewed as preliminary, as it is only based on observations of one live individual. No material was preserved. There were however enough details visible on the live individual and the photographs to recognise this species as belonging to the taxon *Acrumena* Brunet, 1965.

The long and slender, spindle-shaped animal (Figs 7A, 8A) is colourless and without eyes. The proboscis (Figs 7C, 8A: p) is very small, about 1/10 of the total body length. The pharynx (Fig. 8A: ph) is situated around midbody and has a diameter of approximately 1/8 of the body length.

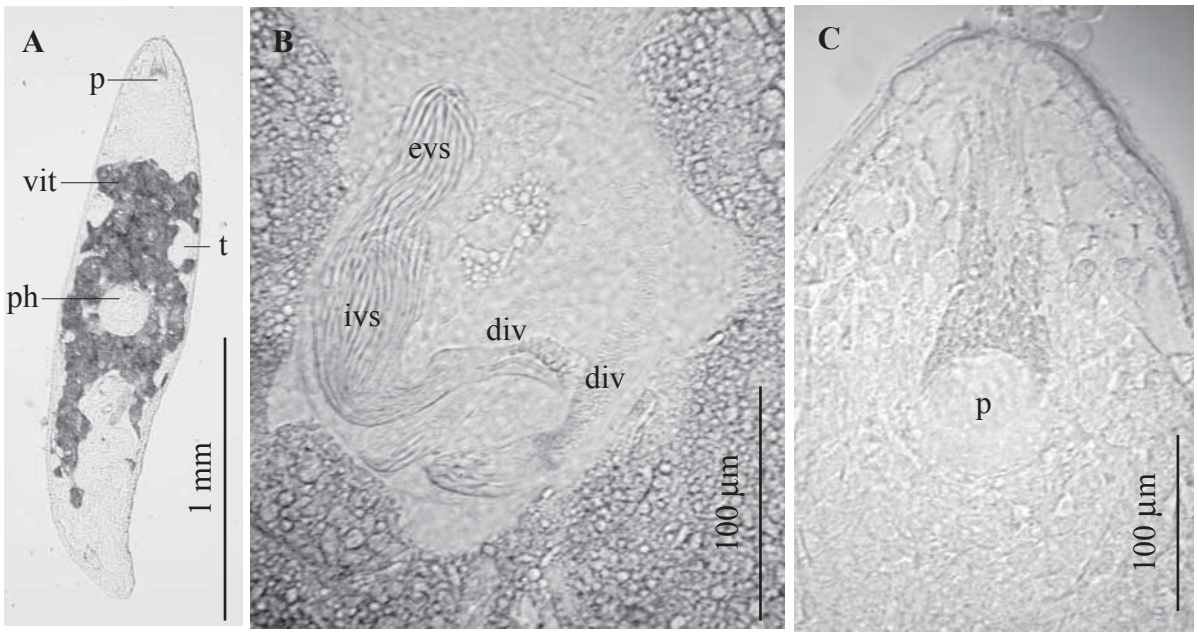

FIGURE 7. *Acrumena* spec. A, Habitus of a live individual. B, copulatory organ (form a live indiviudal). C, proboscis (from a live individual)

The gonopore was not visible, but is most probably situated in the most caudal part of the body. The paired testes (Fig. 8A: t) are very small and situated in front of the pharynx. The ovaries could not be discerned with certainty but are probably situated closely behind the pharynx. The vitellaria (Fig. 8A: vit) are lying close together but there is no indication that they are interconnected. They extend from the level of the testes to that of the copulatory organ, which is situated at approximately 2/3 of the body. Two seminal vesicles (Fig. 8A: evs) enter the copulatory bulb separately, but form a single intracapsular seminal vesicle (Fig. 8A: ivs). In the most distal part of the copulatory bulb two diverticles (Figs 7B, 8A: div) are present. Their exact nature is not clear and should be studied on sectioned material. These diverticles consist of two different parts: a short proximal leaf-shaped part and an elongated tubiform distal part. The latter is probably lined with a glandular epithelium. The copulatory bulb is connected with the gonopore through a very long male atrium (Fig. 8A: ma). A globular uterus (Fig. 8A: ut), lined with slender glands is present near the caudal end of the body.

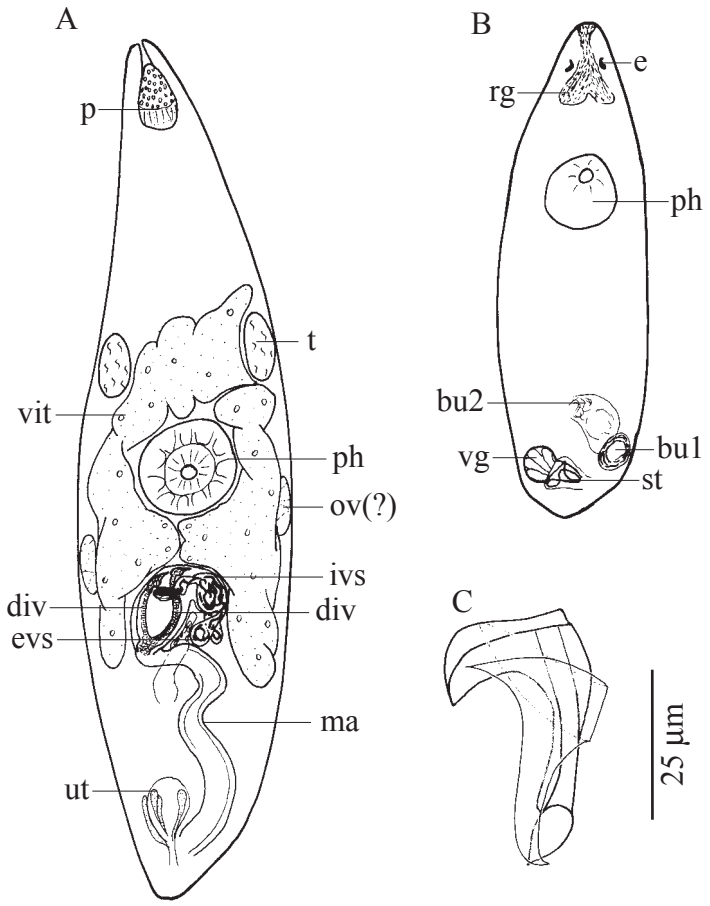

FIGURE 8. *Acrumena* spec. A, General organisation (from a live individual). *Ceratopera* spec. B, general organisation (from a live individual). C, stylet (from a whole-mount).

Discussion. The elongated body shape, small koinocystidid-like proboscis, the general organisation of all organs, the presence of two seminal vesicles and the more detailed structure of the copulatory bulb indicate that this species is a representative of the monospecific taxon *Acrumena* (see Brunet 1965).

There are, however some clear differences between this species and *A. massiliensis* Brunet, 1965 (see Brunet 1965; Karling 1980). The studied individual lacks eyes, whereas these are clearly present in *A. massiliensis* (Brunet, 1965; Karling: unpublished data in coll. SMNH). The vitellaria are much larger and not long and slender as in *A. massiliensis*. The copulatory bulb is situated more anteriorly than in *A. massiliensis* and the male atrium is much longer. Only two diverticles could be observed in this specimen, whereas there are clearly three diverticles present in *A. massiliensis* (Brunet, 1965).

In our view this could easily be described as a new species. We however, refrain from formally describing it as such, because there is no preserved material and some of its features should be studied on sectioned material.

***Ceratopera* spec.**
(Fig. 8B–C)

Locality. Loc. 2.

Material. One animal observed alive and whole mounted (in bad condition).

Description and remarks. The spindle-shaped animal (Fig. 8B) is colourless and has eyes. The pharynx is situated in the first third of the animal and frontal rhabdite-glands (Fig. 8B: rg) are well-developed. The copulatory organ is situated in the most caudal part of the animal and consists of a small prostate vesicle associated with a complex stylet (Fig 8C). This stylet consists of a pointed, 44 µm-long tube and a surrounding mantle. The tubular stylet carries a plate-like flap, which is wider on one side, near the proximal opening of the stylet. The surrounding mantle, which is 38 m long and 24 m wide proximally, consists of two triangular plates, one on each side of the stylet. One of these plates tapers towards the distal tip of the stylet into a slightly bent and pointed tip. A bursa with two different compartments is situated in the caudal part of the body. One of the compartments is globular in shape (Fig. 8B: bu1), and contains coiled-up sperm, whereas the second part of the bursa is sac-like (Fig. 8B: bu2).

This species most likely is a member of the taxon *Ceratopera* Den Hartog, 1964 as the stylet is very similar to that of species included therein (e.g. *C. paragracilis* Ehlers & Ax, 1974; *C. gracilis* (Graff, 1882) Den Hartog, 1964). This taxon contains 12 species, which are characterised by the shape and size of the stylet and the bursal appendage. The latter is however not observed in the severely damaged specimen from Skagerrak. This, together with the limited amount of observations that could be made on the live individual, hampers the identification of this species. Since the stylet is different from every known member of the taxon, this probably constitutes a new species. However, for reasons explained above, we refrain from formally describing it as such.

General remarks

Even though the number of specimens found during this survey was low, the collected material revealed as many as 15 species of Rhabdocoela (incl. two unidentified species). Nine of them are new to the Swedish fauna list and four of these are new to science (see Table 2). With approximately 150 species previously known from Sweden, this means a substantial addition to the Swedish fauna list.

Sampling of marine habitats in Sweden has been ongoing for the past century, especially by Karling (e.g. 1947, 1952b, 1956, 1974), and the marine rhabdocoel fauna of Skagerrak was thought to be rather well known. However, earlier sampling efforts have been concentrating on littoral and sublittoral habitats and never exceeded a depth of 100 m (see Introduction).

Only two of the species found during this campaign were previously known to inhabit deep waters (*M. terminostylus*: 180 m and 300 m by Karling (1956) and *E. norvegica*: 105–120 m by Westblad (1954)). All other collected species are either new to science or only known from shallow habitats.

The large number of Solenopharyngidae among the collected specimens is rather surprising as, up till now, most species of that taxon were mainly found in littoral habitats (e.g. Ehlers 1972, Willems *et al.* 2004b, 2005). There are only a few reports of species occuring sublittoraly: *Culleopharynx armatus* (Riedl, 1956) Ehlers, 1972 was found in the Adriatic Sea between 20 and 40 m (Riedl 1956); *Espegrendia norvegica* was found on the Norwegian coast between 50 and 120 m (Westblad 1954 and this paper); *Trisaccopharynx westbladi* occurs between 20 and 60 m deep in the Swedish Gullmarfjord (unpublished data of Jondelius, Karling and Willems).

Austrorhynchus artoisi **sp. nov.** was collected from between 331–509 m, a depth similar to that where *A. antarcticus*, *A. biserratus* Artois *et al*., 2000, *A. magnificoides* and *A. magnificus* were found (Brunet 1965, Karling 1977, Artois *et al.* 2000). The remaining 12 species of *Austrorhynchus* occur in the tidal zone or sublittorally (max. 32 m) in sandy or muddy bottoms and on algae. Similarly, all 31 species within the taxon *Proxenetes* except two, *Proxenetes flabellifer* Jensen, 1878 (Steinböck 1932: 180 m) and *P. trispinosus* Artois *et al.*, 2000 (Artois *et al.* 2000: 600 m) are found in shallow waters.

The foregoing examples clearly show that sampling in deep waters all over the world can contribute to our

knowledge of the marine rhabdocoel fauna, even in Europe, where the marine rhabdocoels have been studied more extensively than elsewhere.

Acknowledgements

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